

IDENTIFICATION AND TAXONOMIC STATUS OF *CORDYLANTHUS TENUIS*
SUBSP. *PALLESCENS* (OROBANCHACEAE)

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ABSTRACT

Cordylanthus tenuis subsp. *pallescens*, Pallid Bird's-beak, is a rare plant of the Mount Shasta area of northern California. Recent reports of dozens of populations outside its limited expected range, observations of plants with morphology intermediate to other subspecies of *C. tenuis*, and populations that seemed to include individuals of more than one subspecies, raised questions about its rarity and taxonomic validity. Examining populations in the field suggested that many reported populations were misidentified because they were based on a single trait, often foliage color. The name *C. t.* subsp. *pallescens* should be restricted to populations in which all or most plants have the combination of traits expected of this taxon, including yellow-green foliage, four to eight flowers per cluster, and short, mostly non-glandular calyx hairs. In the context of other variation recognized at the subspecies level in *C. tenuis*, recognizing *C. t.* subsp. *pallescens* taxonomically is a reasonable choice, despite its very limited range.

Key Words: *Cordylanthus tenuis* subsp. *pallescens*, intraspecific identification, Orobanchaceae, plants with legal protection, rare plants.

Cordylanthus tenuis A. Gray is a widespread, variable species of the California Floristic Province. Like its congeners, it is an annual hemiparasite that blooms in mid- to late summer. Host plants of *Cordylanthus* Nutt. ex Benth. species are usually trees and shrubs, though herbaceous plants can also be parasitized (Chuang and Heckard 1971). The inflorescence is complex. Each flower is partly hidden between the spathe-like calyx and a similar inner floral bract, and subtended by entire or three-parted (trifid) leaf-like outer bracts (Chuang and Heckard 1976).

Morphological variation within *C. tenuis* has led to the recognition of six intergrading subspecies (Chuang and Heckard 1986). Five of them had previously been recognized at the species level. Two of the subspecies, *C. t.* subsp. *pallescens* (Pennell) T. I. Chuang & Heckard and *C. t.* subsp. *capillaris* (Pennell) T. I. Chuang & Heckard, are rare California endemics on CNPS List 1B.2 (rare, threatened, or endangered), the former with state rank S1.1 (critically imperiled; CNPS 2011) and the latter federally listed as Endangered (U.S. Department of the Interior, Fish and Wildlife Service 1995). *Cordylanthus tenuis* subsp. *pallescens* was described as endemic to the Mount Shasta region of Siskiyou

County, California, from a very small area near the southern base of Black Butte. Two other subspecies also occur in the Mount Shasta region: *C. t.* subsp. *tenuis* and *C. t.* subsp. *viscidus* (Howell) T. I. Chuang & Heckard.

Efforts to protect *C. t.* subsp. *pallescens* became confused when approximately 40 populations were reported from the area south of Dunsmuir to the north side of Mount Shasta and east into the Eddy Mountains (CNPS 2011). These populations were found to be morphologically diverse, potentially confounding attempts to identify populations with legal status. An additional population was reported from Lake County (vouchered by *Isle 1704*, at CHSC). These reports raised questions. Are all the reported *C. t.* subsp. *pallescens* populations correctly identified? Is *C. t.* subsp. *pallescens* distinct enough to consider it a valid taxon? Is *C. t.* subsp. *pallescens* too widespread and common to protect as a rare plant? What are its true geographic range and substrate fidelity? To address these questions, putative populations of *C. t.* subsp. *pallescens* were visited in the field in 2010 and herbarium specimens were examined.

METHODS

Twenty-four *Cordylanthus tenuis* populations were sampled at peak flowering time, 2–10

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TABLE 1. POPULATIONS OF *CORDYLANTHUS TENUIS* SAMPLED IN 2010. n = population size, determined by counting plants in the smaller populations and estimated in the larger populations. rpt = reported as *C. tenuis* subsp. *pallescens* (CNPS 2011).

Site	Location	Date	Latitude	Longitude	Elev. (ft)	County	n	rpt	Subspecies
1	near Black Butte trailhead, on road	2 Aug	41.37476	-122.3368	4375	Siskiyou	7400	x	<i>pallescens</i>
2	south of Black Butte, behind the dump	3 Aug	41.35067	-122.3373	4000	Siskiyou	1363	x	<i>pallescens</i>
3	Road 40N26 in section 25	3 Aug	41.28563	-122.3742	3932	Siskiyou	1454	x	<i>tenuis</i>
4	Road 40N43 at first creek crossing	3 Aug	41.28133	-122.368	3488	Siskiyou	1240	x	<i>tenuis/viscidus</i>
6	Road 40N43, above road	3 Aug	41.26081	-122.4027	4636	Siskiyou	516	x	<i>tenuis</i>
9	Summit Drive, south of Sunrise Drive junction	4 Aug	41.34715	-122.3489	3855	Siskiyou	840	x	<i>pallescens</i>
10	Rd. 41N26, 0.6 miles from Old Stagecoach Rd.	4 Aug	41.40561	-122.4426	3411	Siskiyou	13000	x	<i>tenuis</i>
12	Old Stagecoach Rd., ~1/2 mile N of Eddy Cr. Rd.	4 Aug	41.4128	-122.434	3267	Siskiyou	750	x	<i>tenuis</i> (& one <i>viscidus</i>)
13	Road 43N18, near west end	4 Aug	41.49255	-122.2098	5410	Siskiyou	56	x	<i>pallescens/tenuis</i>
14	near Dunsmuir, Panorama Rd. N of I-5	5 Aug	41.20081	-122.279	2540	Siskiyou	3000	x	<i>viscidus</i>
15	Rd. 1M036 (Railroad Park Rd.) by railroad museum	5 Aug	41.18648	-122.2956	2310	Siskiyou	2000	x	<i>viscidus/tenuis</i>
16	10 mi E of McCloud; jct Rd. 41N06 and Hwy 89	5 Aug	41.26624	-121.9272	3798	Siskiyou	7500	x	<i>viscidus</i>
17	Lake Siskiyou, north shore	6 Aug	41.29067	-122.3615	3270	Siskiyou	900	x	<i>tenuis</i>
18	SE of Lake Siskiyou; Rd. 39N34	6 Aug	41.25272	-122.3512	4164	Siskiyou	5000	x	<i>viscidus/tenuis</i>
19	SE of Lake Siskiyou, Ney Springs Rd.	6 Aug	41.26872	-122.3198	3060	Siskiyou	10000	x	<i>tenuis</i>
20	Hwy 97, at Shasta-Trinity NF sign	6 Aug	41.20736	-121.7824	4449	Siskiyou	500		<i>viscidus</i>
22	Forbestown Rd.	7 Aug	39.49799	-121.3241	2637	Butte	350		<i>viscidus/tenuis</i>
23	Rd 26 near a jct, 3/4 mile (up hill of) Rd 40N43	8 Aug	41.22711	-122.4555	4953	Siskiyou	500	x	<i>tenuis</i>
25	near Black Butte trailhead, on road	9 Aug	41.37442	-122.3335	4400	Siskiyou	7400	x	<i>pallescens</i>
26	Road A10 on Mount Shasta	9 Aug	41.35249	-122.3086	4411	Siskiyou	500	x	<i>tenuis</i>
27	Hotlum; between end of Rd 42N48 and the trestle	9 Aug	41.49143	-122.3035	4160	Siskiyou	193	x	<i>tenuis</i>
28	Weed; by the elementary school	10 Aug	41.42691	-122.3796	3635	Siskiyou	382	x	<i>pallescens?</i>
29	Stewart Springs Rd, 1.5 mile from Gazelle Rd.	10 Aug	41.43601	-122.4668	4000	Siskiyou	4000	x	<i>tenuis</i>
30	Stewart Springs Rd, 5.3 miles from Gazelle Rd.	10 Aug	41.42462	-122.5165	4381	Siskiyou	2000	x	<i>tenuis</i> (& one <i>viscidus</i>)

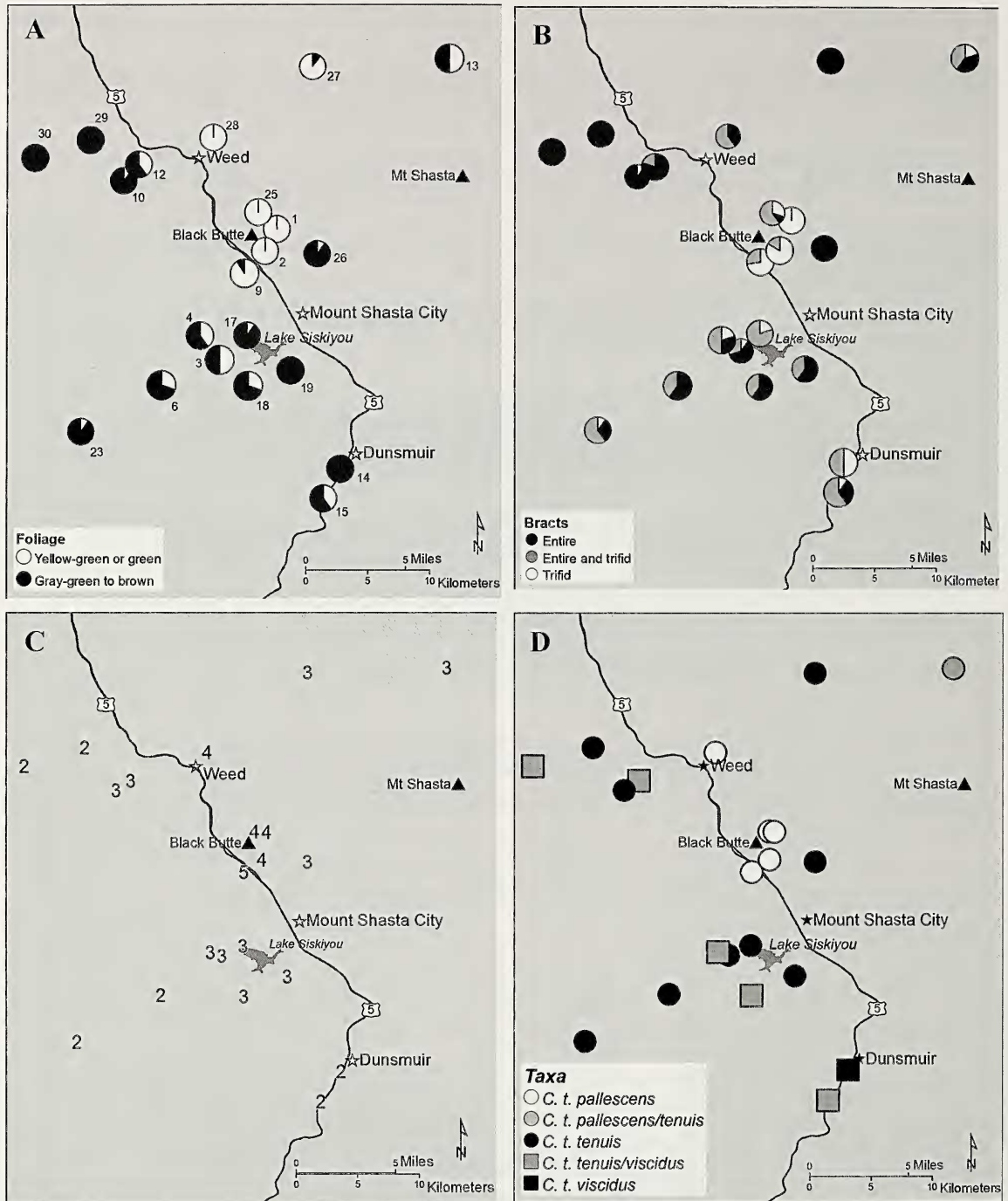


FIG. 1. Location of numbered study sites (A) and frequency of traits and identification of sampled *Cordylanthus tenuis* populations in Siskiyou County, California. A, study site locations and numbers, and foliage color. B, trifold, entire, or both trifold and entire bracts. C, flowers per cluster (mode), in larger clusters. D, subspecific identification.

August 2010 (Table 1, Fig. 1A). Nineteen of the populations sampled were selected from among those recorded as *C. t.* subsp. *pallescens* (CNPS 2011). Additional populations of *C. t.* subsp. *viscidus* to the east of Mount Shasta were sampled for comparison (Table 1). Traits reported to distinguish the subspecies (Chuang and

Heckard 1986) and relatively easy to see in the field were recorded for ten to twelve specimens in each population (Table 2). Foliage color was defined as the overall color of the plant, resulting mainly from the color of leaves, stems, and outer bracts. The samples were selected to include individuals exhibiting obvious extremes in color,

TABLE 2. MORPHOLOGICAL TRAITS RECORDED FROM *CORDYLANTHUS TENUIS* INDIVIDUALS SAMPLED IN THE FIELD, AND THEIR SCORING IN NONMETRIC MULTIDIMENSIONAL SCALING BY POPULATIONS AND INDIVIDUALS.

Trait	Type	Populations	Individuals
Foliage	category	Proportion yellow-green and green / gray-green and maroon	yellow-green or green / gray-green / green with maroon / maroon / solid or dark red brown
Flowers/cluster	count	Proportion; mode 1–3 / more than 3	count (maximum)
Bracts shape	category	Proportion all trifid / all entire / both trifid and entire	
Bracts trifid	category		yes / no
Bracts entire	category		yes / no
Bract tips callused	category	Proportion large / slight / none	yes / no
Bract tips expanded	category	Proportion yes / no	not / slightly / greatly
Calyx color	category	Proportion yellow or slightly maroon-tinged / maroon	maroon / green
Long calyx hairs	category	Proportion with no / few / many	none / short / long
Calyx glands	category	Proportion sparse / moderate / dense	none / sparse / medium / dense
Short calyx hairs	category	Proportion sparse / moderate / dense	none / sparse / medium / dense

flower clustering, and stature. Additional reported *C. t.* subsp. *pallescens* populations were visited but not sampled because they were located near sampled populations and had obviously similar plants.

Plants were identified to subspecies using the available keys (Chuang and Heckard 1986; Chuang and Heckard 1993).

A total of 336 unique *C. tenuis* subsp. *pallescens*, *C. t.* subsp. *tenuis*, and *C. t.* subsp. *viscidus* specimens from CHSC, JEPS, ORE, OSC, UC, and WILLU (abbreviations from Thiers, continually updated) were examined before fieldwork and re-examined after fieldwork (Appendix 1).

Statistical summary and analysis comparing *Cordylanthus tenuis* populations were performed in the R environment for statistical computing (R Development Core Team 2010). The function 'boxplot' was used to generate box-and-whisker plots where the 'hinges' of the boxes represent the first quartile, the median, and the third quartile and are therefore non-parametric. The function 'kruskal.test' was used to perform the Kruskal-Wallis rank sum test on the sampled subspecies of *C. tenuis* but not the 'ambiguous' populations. The Kruskal-Wallis rank sum test is a non-parametric analogue of ANOVA which tests the hypothesis that at least one sampled group is different. To control for multiple comparisons an adjusted p-value was calculated using the method of Benjamini and Hochberg (1995).

To explore multivariate relationships among the *C. tenuis* populations, ordinations were performed on both the individual data as well as population summaries. Ordination of population summaries began with the construction of a matrix of Bray-Curtis distances using the R function 'vegdist' (Oksanen et al. 2011). Non-metric multidimensional scaling (NMS) was performed with the R function 'isoNMS' (Venables and Ripley 2002). The maximum number of

iterations for the algorithm to perform was set to 500, however this maximum was never reached during the analysis. Over 100 ordinations were performed to evaluate the final stress of the result as well as to subjectively judge its stability. The algorithm occasionally settled at a relatively high stress (e.g., around 40) but was typically close to 10 and the plots of these low-stress ordinations appeared fairly consistent. One such ordination was arbitrarily chosen for presentation based on its low stress (9.44%). NMS of *Cordylanthus* individuals was performed using PC-ORD (McCune and Mefford 2006), again using Bray-Curtis distances. 200 iterations were performed, and the final ordination shown represents the result after stress was stabilized at 12.8%.

RESULTS

Plants in some populations could be identified unambiguously as belonging to one of the three *Cordylanthus tenuis* subspecies occurring in the area, but other populations were ambiguous. Plants in sites one, two, nine, and 25 near Black Butte (Table 1, Fig. 1A) were yellow-green and had 4–8 flowers per cluster, short, mostly non-glandular calyx hairs, and trifid bracts, all traits of *C. t.* subsp. *pallescens* (Fig. 1A–C; Chuang and Heckard 1986). These sites are referred to here as the core area. Approximately 8,600 individuals of *C. t.* subsp. *pallescens* grew in these sites (Table 1). The plants of site 28 near the town of Weed were similar except the outer bracts were consistently entire. However, most of the 19 sampled populations that had been reported as *C. t.* subsp. *pallescens* could be readily identified in the field as *C. t.* subsp. *tenuis* or *C. t.* subsp. *viscidus* or intermediate between those subspecies, although they might have a few plants that resembled *C. t.* subsp. *pallescens* (Table 1, Fig. 1D). The population as a whole was not *C. t.* subsp. *pallescens*, though if you looked hard

enough you could see individuals that had a trait like *C. t.* subsp. *pallescens*. Sources of misidentification probably include (1) the relatively glandless inflorescences typical of both *C. t.* subsp. *tenuis* and *C. t.* subsp. *pallescens*, (2) the presence of occasional green plants in nearly all populations visited, and (3) the presence of occasional individuals with four or more flowers per cluster in most populations.

Certain populations could be assigned to *C. t.* subsp. *tenuis* (Fig. 1D). These included populations on serpentine-influenced substrates on the east slope of the Klamath Mountains (sites three, six, 10, 17, 19, and 23), where most flower clusters had one to three flowers, outer bracts mostly entire, and calyces had sparse to moderately dense glands and short to slightly longer eglandular hairs. Most plants were gray-green to brown, although a small minority of plants in most populations were bright or yellow green. Plants at site 26 (A10 road on the west side of Mount Shasta) were similar. The plants near Hotlum, north of Mount Shasta (site 27), also seemed to be *C. t.* subsp. *tenuis* based on their short calyx hairs, lack of glands, and small flower clusters, although they were predominantly yellow-green.

Plants in two more distant populations (site 14 near Dunsuir, 16 km south of Black Butte, and site 16, 32 km to the east) could be assigned to *C. t.* subsp. *viscidus* (Fig. 1D). They had outer bracts that could be trifid or entire, moderately to very dense calyx glands, and mostly longer eglandular calyx hairs. Most plants were gray-green to brown, though a small minority of plants in both populations were bright green.

At some sites south or northwest of Black Butte (sites four, 12, 15, 18, and 30), the plants were intermediate between *C. t.* subsp. *tenuis* and *C. t.* subsp. *viscidus*. At site 13 north of Mount Shasta, plants had a mix of the traits of *C. t.* subsp. *pallescens* and *C. t.* subsp. *tenuis* (Fig. 1D).

The occurrence of selected traits in populations identified to subspecies was compared using boxplots (Fig. 2). Subsequent statistical hypothesis testing demonstrated significant differences among taxa for eight of these traits (Table 3). *Cordylanthus t.* subsp. *pallescens* differed from both of the other subspecies in the occurrence of yellow-green foliage, green or mostly green calyces, flower number per cluster, and presence of long hairs. However, *C. t.* subsp. *pallescens* resembled *C. t.* subsp. *viscidus* in bract shape and resembled *C. t.* subsp. *tenuis* in other traits such as gland density (Fig. 2).

Traits considered typical of *C. t.* subsp. *pallescens* occurred in populations outside the core area, but they did not necessarily all occur together in the same population or the same individual. Occasional individuals with yellow-green foliage were present in most populations (Fig. 1A), and most or all individuals in the two

sampled populations north of Mount Shasta (sites 13 and 27) were yellow-green. Bracts varied from trifid to entire within populations and even within individuals (Fig. 1B). Only in the core area did the majority of plants have all bracts trifid, but several populations outside the core area had a few plants with only trifid bracts and in many populations all or most plants had a mix of trifid and entire bracts (Fig. 1B). Flower clusters with four or more flowers predominated only in the core area plus Weed. In only three sampled populations (sites 14, 15, and 29) did all clusters contain only three or fewer flowers (Fig. 1C).

Traits considered typical of *C. t.* subsp. *pallescens* occurred far from the Mount Shasta area as well. Some herbarium specimens of *C. t.* subsp. *tenuis* collected in Jackson County, Oregon, had the dense glands and long hairs of *C. t.* subsp. *viscidus* but regularly had flower clusters with four to six flowers (e.g., Heckard 2779, Heckard 3151, Rolle 464, Sikes 130, and Waring 742 (all OSC) and Halse 2433 (OSC and ORE). The reported *C. t.* subsp. *pallescens* from Lake County (Isle 1407 [CHSC]) was a green plant with glandular calyces, long calyx hairs, and one to two flowers per cluster, best classified as an unusually green *C. t.* subsp. *viscidus*.

In NMS of *C. tenuis* populations, populations identified as *C. t.* subsp. *pallescens* clustered together as highly positive on axis one and highly negative on axis two (Fig. 3). Populations identified as *C. t.* subsp. *viscidus* were well separated from *C. t.* subsp. *pallescens*. In this example (Fig. 3), sites three (*C. t.* subsp. *tenuis* west of Siskiyou Lake) and 28 (odd *C. t.* subsp. *pallescens* in Weed) cluster together, apparently because plants in both groups have entire bracts and relatively large numbers of flowers per cluster.

Although foliage color is often diagnostic of *C. t.* subsp. *pallescens* (Fig. 2) and is the easiest diagnostic trait to see, it was difficult to score consistently. The darkest plants among the yellow-green *C. t.* subsp. *pallescens* in the core sites were scored as gray-green. On the other hand, nearly all the estimated 5,000 plants at site 19 southeast of Lake Siskiyou were maroon to brown and the few that were less maroon were scored as green, though they were probably darker than any plants in the core area. The proportion of atypically green plants in most sites, or brown ones in site 27 near Hotlum, is exaggerated in the recorded samples of ten plants because we attempted to measure plants representing all the obvious variants. For these reasons, the real difference between populations with mostly yellow-green as opposed to mostly maroon plants (Fig. 1A) is likely greater than reported, and certainly not less.

In NMS of individuals using the same traits as for the NMS of populations (Table 2), some individuals from the core *C. t.* subsp. *pallescens*

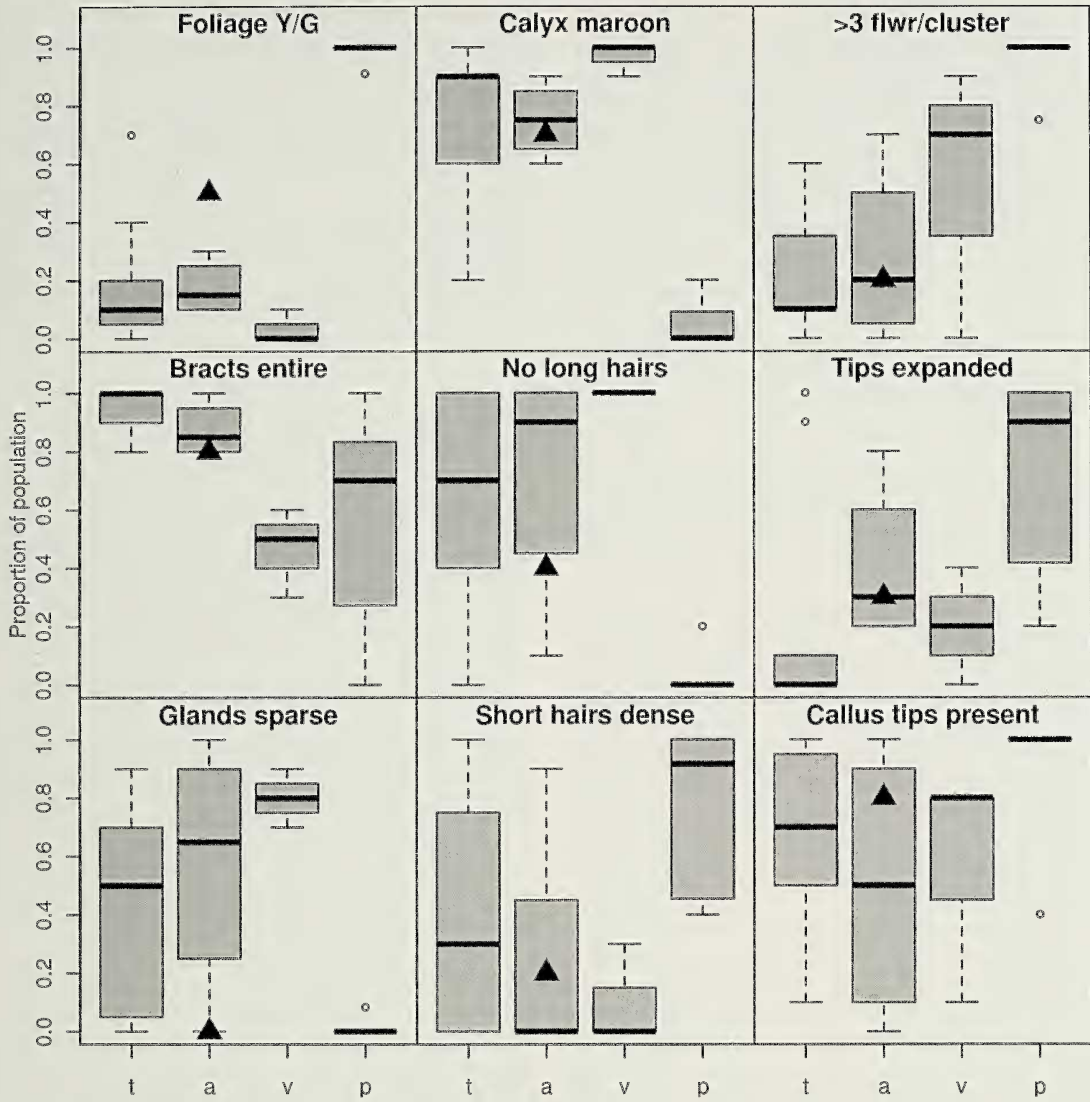


FIG. 2. Boxplots of proportion of each population possessing a trait as a function of taxonomic determination. Populations are indicated as 't' for *C. t.* subsp. *tenuis*, 'a' for ambiguous population determination, 'v' for *C. t.* subsp. *viscidus*, and 'p' for *C. t.* subsp. *pallescens*. Site 13 (43N18 near west end) was excluded from the analysis but represented in the boxplots by a filled triangle in the 'ambiguous' column.

TABLE 3. KRUSKAL-WALLIS RANK SUM TEST OF DIFFERENCES AMONG PUTATIVE *CORDYLANTHUS TENUIS* SUBSPECIES AS A FUNCTION OF TRAITS.

Trait	Kruskal-Wallis chi-squared	df	P-value	Adjusted p-value
Foliage Y/G	12.04414	2	0.002425	0.010753
>3 flowers/cluster	10.95608	2	0.004178	0.010753
Bracts entire	9.712409	2	0.00778	0.014004
Callus tips present	3.241385	2	0.197762	0.197762
Tips expanded	7.124084	2	0.028381	0.03649
Calyx maroon	12.0913	2	0.002368	0.010753
No long hairs	10.68701	2	0.004779	0.010753
Glands sparse	8.690403	2	0.012969	0.019453
Short hairs dense	5.982017	2	0.050237	0.056516

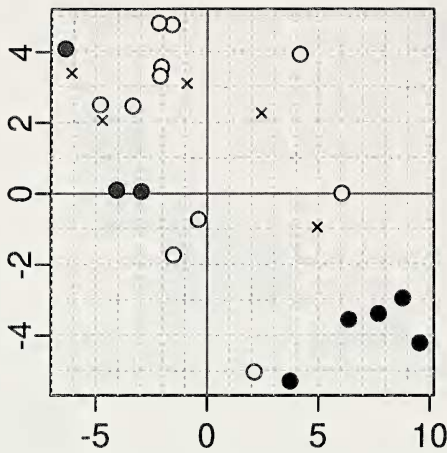


FIG. 3. Non-metric multidimensional scaling axes 1 (x axis) and 2 (y axis) for *Cordylanthus tenuis*. Black = *C. t. subsp. pallescens*, white = *C. t. subsp. tenuis*, and light gray = *C. t. subsp. viscidus*. X = ambiguous population.

populations overlapped some individuals from populations assigned to other taxa, and plants from the Weed populations (site 28) were scattered (results not shown). Because of concern that the scoring of foliage color in some individuals was influenced by the color of most plants in the population, this NMS was repeated omitting that trait from analysis (Fig. 4). With

TABLE 4. FACTOR LOADINGS OF TRAITS ON AXES FOR NMS OF *CORDYLANTHUS TENUIS* INDIVIDUALS, OMITTING FOLIAGE COLOR.

	Axis 1	Axis 2
Flowers/cluster (maximum)	0.14671	0.15412
Bracts trifold	0.06409	0.37117
Bracts entire	-0.06017	-0.22096
Bract tips callused	0.06596	0.16508
Bract tips expanded	0.1275	0.36158
Calyx maroon	-0.26302	-0.25126
Long calyx hairs present	-0.27545	-0.16508
Short calyx hairs (density)	0.19569	0.06919
Calyx glands (density)	-0.19351	-0.11496

foliage color omitted, individuals from the core and Weed populations clustered together, though they were not strongly differentiated from the large cluster of plants from other populations, identified as *C. t. subsp. tenuis*, *C. t. subsp. viscidus*, and intermediates. Axis 1 reflected mainly variation in the calyx (color, and density of hairs and glands) while axis 2 reflected mainly variation in bracts (shape and tips) and calyx color (Table 4).

Cordylanthus tenuis subsp. *pallescens* populations were found along roads (sites one and 25) and in openings in shrub-dominated habitats (sites two and nine) on excessively drained volcanic soils. They were not observed in microsites that

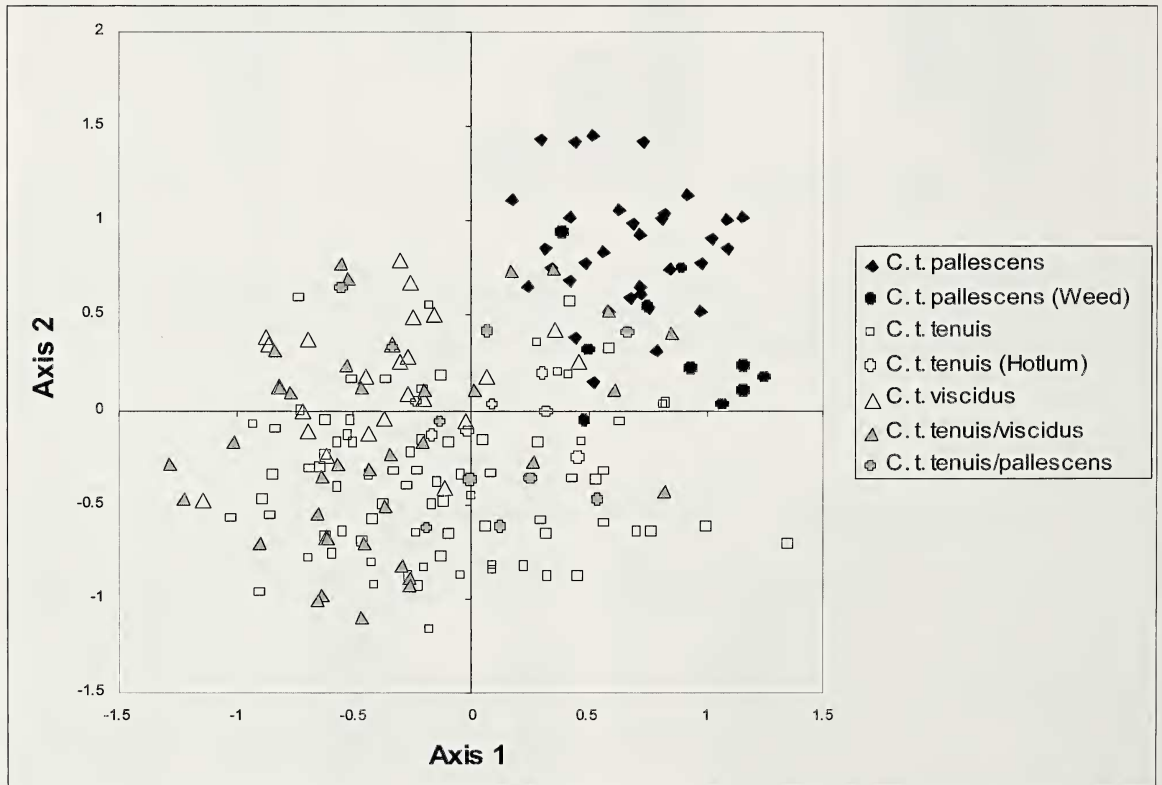


FIG. 4. Non-metric multidimensional scaling for *Cordylanthus tenuis* individuals omitting foliage color.

had thick layers of pine needles, even when they grew in adjacent microsities that had bare mineral soil. They were not found in fully shaded sites. Observed populations of other *C. tenuis* subspecies occurred in similar habitats, though the range of substrates was greater and included serpentine substrates.

Nearly every mature *C. tenuis* flower in the core area and in some of the nearby sites had a hole on the side near the base, where an insect had chewed through the inner bract, calyx, corolla, and ovary wall.

DISCUSSION

Validity of *Cordylanthus tenuis* subsp. *pallescens* as a Taxon

The core *Cordylanthus tenuis* subsp. *pallescens* populations (sites one, two, nine, and 25) appear to form a geographically coherent metapopulation around Black Butte with outlying populations in nearby Weed. These plants probably number in the tens of thousands, growing on a single substrate and characterized by a distinctive combination of morphological traits. They look strikingly different from typical *C. t.* subsp. *tenuis* and *C. t.* subsp. *viscidus*, and were originally described as a species, *C. pallescens* (Pennell 1947). Because some morphologically intermediate plants occur, this taxon was reclassified as a subspecies of *C. tenuis* (Chuang and Heckard 1986). The reported existence of large numbers of plants with intermediate morphology led to the concern that recognizing *C. t.* subsp. *pallescens* taxonomically might be inappropriate (L. W. Heckard, personal communication).

Defining the concept of the species has challenged taxonomists for decades. Many solutions have been proposed (e.g., Mayr 1963; Sokal and Crovello 1970; Wiley 1978; Nixon and Wheeler 1990; Baum and Shaw 1995; Coyne and Orr 2009) but resolution has not been achieved, in part because the need to name species reflects both the pattern of biodiversity and the human need for neat, mutually exclusive names that match the way human minds classify organisms (Hey 2001; Yoon 2009).

Criteria for naming subspecies and varieties are even more vague than criteria for naming species (Haig et al. 2005). Intraspecific names may be applied to incipient species that are morphologically very similar but geographically isolated, or to virtually any grouping within a species that seems identifiable and is of sufficient interest.

Intraspecific groupings differing by a single trait presumably caused by a single gene, such as hairiness (e.g., *Elymus glaucus* [Wilson et al. 2000]), awn length, or flower color are usually not recognized taxonomically. *Cordylanthus tenuis* subsp. *pallescens* is identified by at least four

clusters of traits: foliage color (which may result from gland density), number of flowers per cluster, the density of the various classes of calyx hairs (long non-glandular, short non-glandular, and short glandular hairs), and bract shape (tip traits and perhaps overall trifid/entire shape; Fig. 1B). Although these traits occur together in the core *C. t.* subsp. *pallescens* populations, they occur separately in nearby populations (Fig. 1A–C). Therefore, the name *C. t.* subsp. *pallescens* cannot be dismissed as the inappropriate labeling of a single gene.

Arguments can be made for three taxonomic solutions to the *C. t.* subsp. *pallescens* problem.

Option 1: Synonymize *C. t.* subsp. *pallescens* with one of the other subspecies. It is similar to the other subspecies. Even its most distinctive traits occur at least occasionally in *C. t.* subsp. *tenuis*, *C. t.* subsp. *viscidus*, or both. Clusters of four or more flowers, though otherwise rare in *C. tenuis*, occur in northern populations of *C. t.* subsp. *viscidus* and in *C. t.* subsp. *barbatus* T. I. Chuang & Heckard of the southern Sierra Nevada (Chuang and Heckard 1986). Foliage color seems diagnostic in *C. t.* subsp. *pallescens*, but green plants occur occasionally in populations of the other two *C. tenuis* subspecies in the Mount Shasta area and predominate in the rare *C. t.* subsp. *capillaris* of Sonoma County, California (Chuang and Heckard 1986). Color is known to vary within some related taxa, such as the rare *Chloropyron maritimum* (Nutt. ex Benth.) A. A. Heller subsp. *palustre* (Behr) Tank & J. M. Egger, which is usually brown although individuals and even entire small populations may be green (Tom Kaye, Institute of Applied Ecology, Corvallis, Oregon, personal communication).

The problem with synonymizing *C. t.* subsp. *pallescens* with one of the other *C. tenuis* subspecies is choosing the subspecies with which to synonymize it. The core *C. t.* subsp. *pallescens* cannot easily be included in either *C. t.* subsp. *tenuis* or *C. t.* subsp. *viscidus* because *C. t.* subsp. *pallescens* combines the trifid bracts of *C. t.* subsp. *viscidus* with the short hairs and sparse glands of *C. t.* subsp. *tenuis*, together with yellow-green coloration that is rare in the other subspecies (Fig. 2).

Option 2: Combine *C. t.* subsp. *pallescens*, *C. t.* subsp. *tenuis*, and *C. t.* subsp. *viscidus*. Combining these three subspecies into a single widespread, variable taxon would not only simplify *C. tenuis* taxonomy by removing taxonomic recognition from a small series of odd populations, but also solve two other problems in *C. tenuis* classification. In the Mount Shasta area, some *C. tenuis* plants exhibit traits in combinations not typical of any subspecies, making subspecific identification difficult or impossible (Fig. 1D; Rhonda Posey, personal communication). Morphologically intermediate plants are also common

in the western foothills of the Sierra Nevada (Lawrence Janeway, personal communication). Merging the three subspecies would also do away with the anomalous range of *C. t.* subsp. *tenuis*, widespread in the Sierra Nevada and disjunct in the Trinity Mountains (Chuang and Heckard 1986). However, this change could destabilize the other *C. tenuis* subtaxa including the geographically isolated and federally listed endangered *C. t.* subsp. *capillaris*, because although subspecific taxa can be subjective groupings and the degree of difference between them may vary from species to species, one prefers the subspecific taxa within one species to be equivalently distinct. It would be best to study all six *C. tenuis* subspecies before making such a change.

Option 3: Recognize *C. t.* subsp. *pallescens* as an intraspecific taxon. Subspecific taxa are expected to be a bit fuzzy, to blend in with the relatives at the edges of their range. Individual *C. t.* subsp. *pallescens* traits, such as yellow-green coloration and large flower clusters, are rare in other *C. tenuis* taxa. The combination of traits characteristic of *C. t.* subsp. *pallescens* is rare in populations of the other subspecies even near Mount Shasta and absent or nearly so elsewhere. *Cordylanthus tenuis* subsp. *pallescens* seems to be at least as distinctive as any other *C. tenuis* subspecies currently recognized (Chuang and Heckard 1986). The plants in and near the core *C. t.* subsp. *pallescens* populations appear morphologically similar (this study; Robin Fallscheer, California Department of Fish and Game, personal communication; Robert Hawkins, Timber Products Company, personal communication). Many reports of *C. t.* subsp. *pallescens* or intermediate populations (CNPS 2011) result from misidentified yellow-green plants of *C. t.* subsp. *tenuis* or *C. t.* subsp. *viscidus*. The only problem with recognizing *C. t.* subsp. *pallescens* seems to be that it has such a tiny geographic range that the area of intergradation with other subspecies is larger than its core range.

The pattern of variation that led Chuang and Heckard (1986) to recognize three subspecies in the Mount Shasta area is real (Fig. 1), even though morphologically intermediate plants do occur. Pending a broader study that includes the three *C. tenuis* subspecies that grow outside the geographic region covered in this study, we recommend recognizing *C. t.* subsp. *pallescens* at the subspecific level.

Identification and Management of *C. t.* subsp. *pallescens*

As interpreted in this study, *Cordylanthus tenuis* subsp. *pallescens* is a rare taxon. Rarity can be measured in three basic ways (Rabinowitz 1981). *Cordylanthus t.* subsp. *pallescens* clearly has two of the three; it has a very limited range

and lives in a limited habitat type. Its total population size may be in the tens of thousands, not extremely small but not large for an annual plant.

Cordylanthus tenuis subsp. *pallescens* is more geographically restricted than some earlier reports suggest, extending from just south of Black Butte to the town of Weed in the Southern Cascade Range of Siskiyou County. Much of its range lies on private land managed for timber production (Robin Fallscheer, California Department of Fish and Game, personal communication). Silvicultural practices applied in this area in recent years may have created favorable conditions for this plant, at least for short periods of time, by opening the canopy and disturbing the duff layer. The number of *C. t.* subsp. *pallescens* populations appears to have increased over the last twenty years because plants appear in logging roads, along road edges, and on skid roads where they were not previously observed. Once established, these populations increase exponentially at least for a few years, and sometimes expand into adjacent regenerating clearcuts (Robert Hawkins, Timber Products Company, personal communication).

Cordylanthus tenuis populations commonly grow along roadsides, presumably from seeds moved by road maintenance equipment. It is possible that *C. t.* subsp. *pallescens* was more geographically isolated and more neatly set off morphologically from other *C. tenuis* populations before extensive road construction allowed the three subspecies present in the Mount Shasta area to expand their ranges and establish contact with each other.

Nearly all the mature *C. t.* subsp. *pallescens* flowers observed and most of the flowers in other nearby *C. tenuis* populations had been chewed near the base, through the inner bract, calyx, corolla, and ovary wall, perhaps by an insect eating the ovules. The effect of this predation on seed set could not be determined during this study, because the plants were at anthesis.

Thinking in terms of populations rather than individuals is important when attempting to find and manage *C. t.* subsp. *pallescens* populations. In a *C. t.* subsp. *pallescens* population, all or most of the individuals have all these traits: yellow-green foliage and calyx, clusters of four or more flowers, and sparse calyx glands. Their nonglandular calyx hairs consist of a carpet of very short hairs and very few longer hairs that are perhaps two or three times as long as the short hairs. In most populations, some or all of the outer bracts are trifold.

The plants of site 28 in the town of Weed seemed to be *C. t.* subsp. *pallescens* except that they had entire bracts. Bract shape may be less consistent than its use in classifying *Cordylanthus* species suggests (Chuang and Heckard 1975).

Classifying the Weed population as *C. t.* subsp. *pallescens* is reasonable.

Possession of only one *C. t.* subsp. *pallescens* trait does not make a plant *C. t.* subsp. *pallescens*. Thus, a green *C. tenuis* is not necessarily *C. t.* subsp. *pallescens*. Similarly, the presence of one individual that might be classified as *C. t.* subsp. *pallescens* does not make the population *C. t.* subsp. *pallescens* or a priority for protection. If most of the plants in the population seem to be *C. t.* subsp. *tenuis*, *C. t.* subsp. *viscidus*, or intermediate between those two, the population should not be classified as *C. t.* subsp. *pallescens*. In such a population, the combination of genes producing the single *C. t.* subsp. *pallescens*-like individual would likely be broken up in the next generation, and might reappear again in later generations.

The genes producing the more distinctive *C. t.* subsp. *pallescens* traits seem to be moving out into other *C. tenuis* populations, probably creating novel combinations that will affect the evolution of the species. This may be an interesting process to watch, but we do not see a reason for humans to try to control it by protecting populations that produce only occasional plants that might be identified as *C. t.* subsp. *pallescens*. Protecting the populations that are clearly *C. t.* subsp. *pallescens* (the core populations in this study, plus other populations on nearby Forest Service and private lands) should help assure the continued survival of this taxon.

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- Cordylanthus tenuis* subsp. *pallescens*viscidus. USA. California. Siskiyou Co.: Weed, 3200 ft, 26 Aug 1914, *Heller 11723* (OSC, UC).
- Cordylanthus tenuis* subsp. *tenuis*. USA. California. Eldorado Co.: at lower end of Tamarack Trail, Glen Alpine Canyon, just sw of Leaf Lake, 7000 ft, 16 Aug 1952, *Bacigalupi 930* (OSC). Lassen Co.: on road from Janesville to Thompson Peak, Sierra Nevada, Diamond Range, 5700 ft, 31 Jul 1973, *J. T. Howell and True 50019* (JEPS, OSC). Plumas Co.: SW of Bucks Lake (NE of Frenchman Hill), 5600 ft, 28 Jul 1994, *Ahart 7529* (JEPS). Siskiyou Co.: 2.2 mi n Scott Mt. summit (on Hwy 3, at road junction), 4500 ft, 26 Jul 1987, *Ertter 7325* (OSC, UC); Wagon Creek on E side of Mt Eddy, ca 4 airmiles W. of Mt Shasta City, 5800 ft, 14 Jul 1990, *Ertter 9348* (UC); e side of Mt. Eddy, 4500 ft, 28 Aug 1914, *Heller 11744* (OSC, UC); Shasta-Trinity National Forest, along road 40N26 w of Lake Siskiyou; T32N R6W S25; study site 3, 41.28563°N 122.37418°W, 3932 ft, 3 Aug 2010, *Wilson and Brainerd 16190* (OSC); Shasta-Trinity National Forest, along road 40N26 w of Lake Siskiyou; T32N R6W S25; study site 3, 41.28563°N 122.37418°W, 3932 ft, 3 Aug 2010, *Wilson and Brainerd 16191* (OSC); Forest Service Rd 41N26, the Eddy Creek Rd, 2.8 mile above the junction with Old Stagecoach Rd; study site 11, 41.39273°N 122.47898°W, 4200 ft, 4 Aug 2010, *Wilson and Brainerd 16205* (CHSC, STNF); Forest Service Rd 41N26, the Eddy Creek Rd, 2.8 mile above the junction with Old Stagecoach Rd; study site 11, 41.39273°N 122.47898°W, 4200 ft, 4 Aug 2010, *Wilson and Brainerd 16206* (OSC, UC); Old Stagecoach Rd, about 0.5 mile n of Forest Service Rd 41N26, the Eddy Creek Rd; study site 12, 41.41280°N 122.43398°W, 3267 ft, 4 Aug 2010, *Wilson and Brainerd 16210* (CHSC, DAV, OSC, UC); Ney Springs Rd e of Lake Siskiyou; intermittent along road starting 0.6 miles e of Rd 20M020 and extending at least 0.6 mile; study site 19, 41.26872°N 122.31984°W, 3060 ft, 6 Aug 2010, *Wilson and Brainerd 16233* (OSC); on road 26 between Lake Siskiyou and Gumboot Lake, at a junction about 3/4 mile uphill of Rd 40N43; study site 23, 41.22711°N 122.45552°W, 4953 ft, 8 Aug 2010, *Wilson and Brainerd 16255* (CHSC, DAV, STNF, UC); Shasta-Trinity National Forest; road A10 between town of Mount Shasta and Panther Meadow; study site 26, 41.35249°N 122.30864°W, 4411 ft, 9 Aug 2010, *Wilson and Brainerd 16281* (CHSC, DAV, STNF, UC); Shasta-Trinity National Forest near Hotlum, along dirt road paralleling the railroad track, between Rd 42N48 and the trestle, n of Mount Shasta; study site 27, 41.49153°N 122.30346°W, 3900 ft, 9 Aug 2010, *Wilson and Brainerd 16290* (STNF); Stewart Springs Rd 1.5 miles from the Gazelle Rd; study site 29,

APPENDIX 1

Specimens examined. Herbarium acronyms follow Thiers (continually updated) except that STNF = Shasta-Trinity National Forest. The Wilson and Brainerd specimens cited were collected for this study and recently distributed to the herbaria cited.

Cordylanthus tenuis subsp. *pallescens*. USA. California. Siskiyou Co.: just s Weed Elementary School (s side of Hilltop Dr, less than 0.1 mi e of S. Davis Ave.), Weed NW Quadrangle, 3520 ft, 1 Aug 1990, *Burk DB17* (JEPS); near sw base Black Butte (along hwy 5), 3500 ft, 21 Jul 1975, *Chuang and Chuang 7546* (JEPS); sw of Black Butte, nw of Mt. Shasta City, 41.33°N 122.35°W, 3500 ft, 21 Aug 1969, *Chuang and Heckard 6741* (CHSC, JEPS); w Mt. Shasta City (se of Black Butte, along garbage disposal road just off hwy 5 [old 99]), 3850 ft, 3 Jul 1968, *Heckard and Chuang 1972* (JEPS); ca. 2 mi ne Mt. Shasta City (between old hwy 99 and new freeway), 15 Aug 1971, *Heckard and Chuang 2774* (JEPS); 4 mi nw of City of Mount Shasta (sw of Black Butte, along Garbage Disposal Road just off Highway 5 [old 99]), Garbage Disposal Rd, 3850 ft, 12 Aug 1968, *Heckard et al. 2122* (JEPS); ca. 4 mi nw Mt. Shasta City, s of Black Butte, 0.1 mi from road paralleling old US Hwy 99, along Pony Trail Dr, near Shasta Abbey (Zen Mission), 3900 ft, 4 Aug 1972, *Heckard 3150* (JEPS); n Mt. Shasta City (just sw of Black Butte, corner of old Hwy 99 and Pony Tail Dr.), 3000 ft, 16 Aug 1979, *Heckard 5157* (JEPS); near Miner's Peak (=Black Butte, w side of Mt. Shasta), Upton Plateau, 1 Jul 1894, *Jepson 21345* (JEPS); N of Mt. Shasta City, Siskiyou Co., 19 Jul 1940, *Pennell 26184* (UC); Shasta-Trinity National Forests, se of County Dump site, 41.35°N 122.34°W, 1200 m, 2 Aug 1994, *Ulloa-Cruz 42* (CHSC); road to trailhead for Black Butte Trail; study site 1, 4375 ft, 2 Aug 2010, *Wilson and Brainerd 16186* (DAV, OSC, STNF, UC); s of Black Butte, e of the

41.43601°N 122.46681°W, 9 Aug 2010, *Wilson and Brainerd 16291* (CHSC, DAV, STNF, UC); Forest Service Rd 41N26, the Eddy Creek Rd, 0.6 mile above the junction with Old Stagecoach Rd; study site 10, 41.40562°N 122.44258°W, 3411 ft, 4 Aug 2010, *Wilson and Brainerd 16202B* (OSC); Shasta-Trinity National forest, on Stewart Springs Rd (Forest Service Rd 17) 5.3 miles from the Gazelle Rd, study site 30, 41.42462°N 122.51649°W, 4281 ft, 9 Aug 2010, *Wilson and Brainerd 16291B* (CHSC, DAV, UC). **unknown Co.:** Sierra Nevada Mountains, 19 Sep 1882, *Pringle s.n.* (OSC).

***Cordylanthus tenuis* subsp. *tenuispallescens* intermediate.** USA. California. **Siskiyou Co.:** Shasta-Trinity National Forest; n of Mount Shasta itself, near the w end of Forest Service Rd 43N18, study site 13, 41.49203°N 122.20539°W, 5400 ft, 4 Aug 2010, *Wilson and Brainerd 16214* (STNF); Shasta-Trinity National Forest; n of Mount Shasta itself, near the w end of Forest Service Rd 43N18, study site 13, 41.49203°N 122.20539°W, 5400 ft, 4 Aug 2010, *Wilson and Brainerd 16216* (OSC).

***Cordylanthus tenuis* subsp. *tenuisviscidus*.** USA. California. **Butte Co.:** Forbestown Rd, 39.49799°N 121.32413°W, 2647 ft, 7 Aug 2010, *Wilson and Brainerd 16244* (CHSC, DAV, OSC, UC). **Siskiyou Co.:** Shasta-Trinity National Forest, along Rd 40N43 w of Lake Siskiyou; at first creek crossing w of junction with road 26; study site 4, 41.28133°N 122.36802°W, 3488 ft, 3 Aug 2010, *Wilson and Brainerd 16192* (OSC); Dunsuir, road 1M036 (railroad Park Rd) across form the railroad museum, study site 15, 41.18648°N 122.29558°W, 2310 ft, 5 Aug 2010, *Wilson and Brainerd 16221* (CHSC, DAV, OSC, STNF, UC).

***Cordylanthus tenuis* subsp. *viscidus*.** USA. California. **Butte Co.:** 2.2 mi sw of and below NimsheW (along Humbug Rd on the eastern canyonside of Butte Creek), Butte Creek, 2000 ft, 26 Jul 1957, *Bacigalupi and Whisler 6038* (JEPS); Butte Meadows, 4500 ft, 26 Jul 1957, *Bacigalupi and Whisler 6045* (JEPS); 0.2 mi below junction of Ridge Rd on Humbug Rd (near NimsheW [nw of Magalia]), 2100 ft, 20 Aug 1969, *Chuang and Heckard 6738* (JEPS); Jonesville, 1650 m, 29 Jul 1929, *Copeland 469* (OSC, UC); NimsheW (site), nw of Magalia, 2800 ft, 15 Aug 1971, *Heckard and Chuang 2766* (JEPS); South entrance Manzanita Street (to Stirling City), 3500 ft, 15 Aug 1971, *Heckard and Chuang 2767* (JEPS); 1.5 mi w Butte Meadows (at Thatcher Ridge Rd junction), 4200 ft, 15 Aug 1971, *Heckard and Chuang 2768* (JEPS); Little Summit, 4800 ft, 22 Jul 1914, *Heller 11586* (UC). **Del Norte Co.:** divide between Smith River and south fork of Smith River, French Hill, 17 Aug 1927, *Applegate 5244* (UC); Old Gasquet Toll Rd, Danger Point Ridge top Danger Point, 1425 ft, 19 Jun 1975, *Barker 957b* (JEPS); French Hill Rd, 3.3 miles up from junction with Hwy 99 w of Gasquet; T17N R2E S31, 1700 ft, 28 Jul 1983, *Chambers 5100* (OSC); up the Illinois River beyond Takilma, 24 Aug 1929, *Henderson 11530* (OSC); State line n of Monumental, 3100 ft, 9 Jul 1940, *Tracy 16683* (JEPS, UC); Summit Valley Mountain, 3500 ft, 4 Jul 1938, *van Deventer 130* (JEPS). **Eldorado Co.:** 1.7 mi ne Georgetown, 2800 ft, 20 Aug 1969, *Chuang and Heckard 6732* (JEPS). **Humboldt Co.:** Grouse Creek, 1 Aug 1888, *Chesnut s.n.* (UC); Pine Point Ridge sw Mt. Lassic Lookout, North Coast Ranges, 14 Jul 1949, *Hoffman 3063* (JEPS, UC); Koby Ranch, on road between Willow Creek (on Three Creeks), Koby Ranch,

2000 ft, 20 Jul 1924, *Tracy 6735* (JEPS, UC); Salmon Summit, 5800 ft, 30 Jul 1935, *Tracy 14354* (UC); South Fork of Trinity River (mountain slopes w of its mouth), 1000 ft, 14 Aug 1938, *Tracy 16118* (JEPS, UC); Grouse Mountain, 5000 ft, 16 Aug 1939, *Tracy 16418* (JEPS, UC); ridge top 1 mi w Mud Springs, Trinity Summit, 3800 ft, 24 Aug 1947, *Tracy 17884* (UC); Mud Springs Trinity Summit, 4400 ft, 4 Aug 1949, *Tracy 18411* (UC); Mud Springs Trinity Summit, 4400 ft, 4 Aug 1949, *Tracy 18412* (UC); Mud Springs Trinity Summit, 4400 ft, 4 Aug 1949, *Tracy 18413* (UC). **Lake Co.:** Crooked Tree Ridge Snow Mt. (nw side of mt.), 5400 ft, 7 Jul 1982, *Heckard and Hickman 5965* (JEPS); Mendocino National Forest, North Coast Ranges, Rice Fork Watershed, On Mason Trail to Poges Peak on block spur just n of clear cut, 3120 ft, 28 Jul 1999, *Isle 1407* (CHSC). **Mendocino Co.:** just ne Ham Pass (ca 12 air mi ne of Covelo), Pine Ridge, 4900 ft, 5 Sep 1975, *Heckard and Ashton 4115* (JEPS); **Modoc Co.:** Big Valley Mts., n.d., *Nutting s.n.* (UC). **Plumas Co.:** SW of Bucks Lake (NE of Frenchman Hill), 5600 ft, 28 Jul 1994, *Ahart 7529* (JEPS); e and above Squirrel Creek (ne corner of jct 25N42 and 401, ca 3 air mi n of Spring Garden on Hwy 70), Spring Garden quad, 4500 ft, 21 Jul 1981, *M. S. Taylor 4081* (JEPS). **Shasta Co.:** Lassens Peak, 1 Aug 1896, *Austin 411* (UC); Pinewood Bear Valley Mts., 6000 ft, Jun–Aug 1893, *Baker s.n.* (UC); e of junction with Inwood-Whitmore Rd (along route 44), 3000 ft, 21 Jul 1975, *Chuang and Chuang 7543* (JEPS); 4.5 mi n Pollard Flat (Highway 5), 21 Aug 1969, *Chuang and Heckard 6740* (JEPS); along Route 44 0.4 mi e of junction with Inwood-Whitmore Rd Route 44, 2900 ft, 15 Aug 1971, *Heckard and Chuang 2771* (JEPS); 5 mi se Siskiyou County Line (Hwy 89 ca 1 mi se Dana Rd [A-19] jct), 1340 m, 15 Jul 1990, *Heckard and Chuang 6765* (JEPS); ¼ mi w Dana Rd Junction (along U.S. Highway 89), 4000 ft, 3 Aug 1971, *Heckard and Rubtsoff 2700* (JEPS); 0.2 mi w of junction with McArthur Rd (along highway 89), 4000 ft, 13 Aug 1968, *Heckard et al. 2125* (JEPS); 2 mi e of junction with road to Inwood (along Highway 44, around Northern Pines Motel), 3200 ft, 14 Aug 1968, *Heckard et al. 2129A* (JEPS); along trail to Castle Dome near junction of trail to Indian Springs (Castle Crags State Park), Castle Crags State Park, 4700 ft, 14 Aug 1967, *Heckard 1733* (JEPS); Upper Fall River Valley, 3400 ft, 11 Aug 1914, *Jepson 5773* (JEPS); n Lamoine (along Shotgun Creek), Shotgun Creek, 1700–2000 ft, 19 Jul 1940, *Pennell 26189* (JEPS, UC); 3 mi s Hat Creek (Route 89), 3800 ft, 20 Jul 1940, *Pennell 26208* (UC); 5.6 mi n Pollard Flat Guard Station (on U.S. Highway 99), 5 Sep 1956, *Raven 10472* (JEPS); Lassen National Forest; Red Mountain, along road 34N19, 40.77773°N 121.53062°W, 4706 ft, 6 Aug 2010, *Wilson and Brainerd 16235* (CHSC, DAV, OSC, STNF, UC). **Siskiyou Co.:** 1/2 mi w Hamburg (along hwy following Klamath River), 1500 ft, 12 Aug 1954, *Bacigalupi et al. 4792* (JEPS); on road from Callahan to Carrville (1.2 mi above [and s of] junction with Gazelle road, lower part of grade over Scott Mt.), 3600 ft, 13 Aug 1954, *Bacigalupi et al. 4795* (JEPS); 0.3 mi below Gumboot Creek crossing (both sides of rd 40N26), The Eddy's, 5600 ft, 18 Aug 1990, *Burk s.n.* (JEPS); w Dunsuir (n side of road 40N26, ca. 1.8 mi below South Fork Sacramento River Bridge), Shasta National Forest, 6000 ft, 3 Nov 1990, *Burk s.n.* (JEPS); near Shackelford Creek, Quartz Valley, 11 Aug 1908, *Butler 25* (UC); s side Dunsuir, 2500 ft, 21 Jul 1975, *Chuang and*

Chuang 7545 (JEPS); 1/2 mi w Hamburg (on Hwy 96 above the Klamath River), 1400 ft, 21 Aug 1969, *Chuang and Heckard 6742* (JEPS); 27 mi n Happy Camp (Elder Mt Rd junction, on road to O'Brien), 2700 ft, 21 Aug 1969, *Chuang and Heckard 6743* (JEPS); Shasta Springs, 2 Sep 1917, *Eastwood 6664* (UC); n side Mt. Shasta (along Bolam logging road at e-w fork), 4800 ft, 2 Jul 1968, *Heckard and Chuang 1971* (JEPS); 1 mi s of downtown Dunsmuir (below freeway), 2700 ft, 15 Aug 1971, *Heckard and Chuang 2773* (JEPS); just a mile over s of downtown Dunsmuir (along Dunsmuir Ave), 2700 ft, 13 Aug 1968, *Heckard et al. 2123* (JEPS); 13 1/2 mi w Shasta County Line (5 1/2 mi w of Medicine Lake junction, along Hwy 89), 3500 ft, 13 Aug 1968, *Heckard et al. 2124* (JEPS); 15 air mi e Montague (Ball Mt. Rd, nw of Goosene Mt), 3800 ft, 18 Jul 1978, *Heckard et al. 4873* (JEPS); n side Mt. Shasta (along Bolam logging road), 5000 ft, 5 Jul 1967, *Heckard 1603* (JEPS); 5.3 mi s Callahan (3 mibelow road summit, along road up to Scott Mt.), 4400 ft, 28 Aug 1971, *Heckard 2784* (JEPS); southern edge Dunsmuir (near first Dunsmuir freeway exit), 2700 ft, 4 Aug 1972, *Heckard 3149* (JEPS); sw Weed (s of Edgewood, road below Stewart Springs), 3200 ft, 7 Sep 1978, *Heckard 4973* (JEPS); s Edgewood (road above Stewart Springs, on Deadfall Meadow-Mt. Eddy Rd.), 4500 ft, 7 Sep 1978, *Heckard 4974* (JEPS); 1 mi s of downtown Dunsmuir (below Hwy 5), 2700 ft, 28 Aug 1979, *Heckard 5160* (JEPS); w Sisson, Mt. Eddy, 6500 ft, 16 Jul 1918, *Heller 13034* (UC); 17.2 mi n of Klamath River, western Cedar Camp Rd, 11 Jul 1950, *Hoffman 3720* (JEPS); Area several miles w of Weed, 41.43°N–122.39°W, 2 Sep 1978, *Jokerst 152* (CHSC); 3 mi se Scott Mountain Lodge (ridge between Mill and Mule Creeks), Scott Mts., 1340 m, 8 Aug 1938, *Keck 4863* (UC); 5 mi s of summit of road from Happy Camp CA to Waldo, OR, 16 Jul 1950, *Mason 14064* (JEPS, UC); North Fork of Sacramento River, 4500 ft, 5 Sep 1956, *Raven 10469* (JEPS); mouth of river Northern Coast Ranges, Salmon River, 800 ft, 14 Aug 1920, *Tracy 5351* (UC); Dunsmuir; Panorama Drive n of Interstate Highway 5, 41.20081°N 122.27902°W, 2540 ft, 5 Aug 2010, *Wilson and Brainerd 16220* (CHSC, DAV, OSC, STNF, UC); Shasta-Trinity National Forest, about 10 miles e of McCloud, at junction of Highway 80 and Forest Service Rd 41N06, 41.20081°N 121.27902°W, 2540 ft, 5 Aug 2010, *Wilson and Brainerd 16222* (CHSC, DAV, STNF, UC); North Shore Rd, n side of Lake Siskiyou, 1.2 miles w of cross road; study site 14, 41.29067°N 122.35152°W, 3270 ft, 6 Aug 2010, *Wilson and Brainerd 16231* (OSC); at sign at border of Shasta-Trinity National Forest on Highway 89 e of McCloud; study site 20, 41.20736°N 121.7824°W, 4449 ft, 6 Aug 2010, *Wilson and Brainerd 16234* (CHSC, DAV, OSC, UC). **Tehama Co.:** Pine Creek, ca. 8 miles w of Cottonwood; along Benson Rd, 600 ft, 10 Jun 1997, *D. W. Taylor 16049* (JEPS); 1 mi e Lyonsville road junction (on route 36, w of Mineral), 4000 ft, 15 Aug 1971, *Heckard and Chuang 2769* (JEPS); ca 0.5 mi from Regan Meadow (along road from Regan Meadow to Brushy Mountain), Shasta Trinity National Forest, 4600 ft, 27 Jul 1979, *Nelson et al. 5047* (JEPS). **Trinity Co.:** on bank above trail to Chloride Mine, Trinity Mountains, Dedrick, 3000 ft, 3 Aug 1948, *Alexander and Kellogg 5385* (UC); along road to Stuart Gap 0.1 mi

se jct with Rd. 30 (Mad-Wildwood Rd.), Devils Camp, 1160 m, 28 Jul 1988, *Dean 155* (UC); Boulder Creek Basin, along trail ca. 0.25 mile from Canyon Creek, 41°N, 123°W, 5200 ft, 8 Aug 1970, *Ferlatte and Howard 275* (OSC); ca 0.25 mi from Canyon Creek (along trail), Trinity Alps, Boulder Cr. Basin, 41°N 123°W, 5200 ft, 8 Aug 1970, *Ferlatte and Howard 1275* (JEPS); about 2 mi se Wildwood (on Peanut-Beegum rd), 3500 ft, 10 Sep 1971, *Heckard et al. 2797* (JEPS); 2.7 mi e Hayfork post office, 2400 ft, 10 Sep 1971, *Heckard et al. 2800* (JEPS); n Trinity Center (1/2 mi s of junction of road to Castella), 2900 ft, 28 Aug 1971, *Heckard 2785* (JEPS); about 4 mi below (s) road summit over Scott Mt., 3800 ft, 28 Aug 1971, *Heckard 2784A* (JEPS); about 2 mi s road junction to Deadfall Lakes (along Scott Mt.-Trinity Center road [about 8 mi s of Scott Mt. road summit]), 3800 ft, 28 Aug 1971, *Heckard 2784B* (JEPS); Red Mountain Trail, 5000 ft, 20 Aug 1953, *Pollard* (JEPS); 2 mi e Burnt Ranch, Spellenberg property, 1600 ft, 13 Aug 1965, *Spellenberg 1225* (UC); sw Wildwood (crest of ridge at head of gulch), Muldoon Gulch, 4200 ft, 19 Aug 1972, *Stebbins* (JEPS). **unknown Co.:** Head of Rush Creek, 5600 ft, 20 Jul 1914, *Yates 537* (UC).

USA. Oregon. Curry Co.: Sourdough Trail in Lemmingsworth Gulch area; area is reached by For. Serv. roads #3907 and #4014, 42.0159°N–124.0033°W, 15 Jul 1979, *Hess s.n.* (OSC). **Jackson Co.:** along Lewis Rd on the ne end of Lost Creek Lake, one mile sw of State Hwy. 62, 42.7009°N–122.6084°W, 555 m, 29 Jul 1981, *Halse 2433* (ORE, OSC); along Lewis Rd on the nw end of Lost Creek Lake, one mile sw of State Hwy. 62, 42.7009°N–122.6084°W, 555 m, 29 Jul 1981, *Halse 2433* (OSC); about 1 mile w of Prospect, 42.7511°N–122.5076°W, 27 Aug 1971, *Heckard 2779* (OSC); Along Crater Lake Rd, 14 miles ne of Trail (2 miles w of Laurelhurst State Park), 2100 ft, 4 Aug 1972, *Heckard 3151* (OSC); part way up Ashland Butte, s. Oregon, 8 Jul 1886, *Henderson 784* (OSC); Ashland, 6 May 1887, *Henderson s.n.* (ORE, OSC); along Ashland-Klamath Falls road 25 mi. E of Ashland, 22 Aug 1916, *Peck 2413* (WILLU); about 1/3 mile w of confluence of Steve Fork and Sturgis Fork, 42.0741°N 123.2196°W, 18 Jul 1991, *Rolle 464* (OSC); Butte Falls Resource Area (Medford District Bureau of Land Management), Bieber Wasson. BLM land accessed by gravel road off of Salt Creek Rd. Within BLM fuels treatment unit BW304, 42.4694°N–122.571°W, 19 Jun 2004, *Sikes 130* (OSC); no locality, 13 Jul 1967, *Waring 742* (OSC). **Josephine Co.:** Wimer Rd, 3. 6 mi. SW of O'Brien, at Rock Ck. bridge, 28 Jul 1983, *Chambers 5110* (OSC); 1.8 miles sw of O'Brien on Oregon Mountain Rd, 21 Aug 1969, *Chuang and Heckard 6744* (OSC); Elder Creek Trail, Siskiyou Forest, 22 Aug 1919, *Ingram 1034* (OSC); Illinois Valley, Rough and Ready Creek, 26 Jun 1990, *Kagan 6269001* (OSC); Grants Pass, 6 Jul 1909, *Peck 2407* (WILLU); mountains near Cal. line, sw of Waldo, 4 Aug 1913, *Peck 2408* (WILLU); near Ore-Cal line along Grants Pass-Crescent City Rd, 2 Jul 1918, *Peck 8100* (WILLU); Takilma, 8 Jul 1918, *Peck 8423* (WILLU). **Lane Co.:** Young Rk. trail 3685. ca. 60 mi. se of Eugene; ca. 20 mi. se of Hills Crk. Res. Approx. 1/6 mi. from where the trail crosses Spur Rd. #435, 43.5207°N–122.4005°W, 30 Jul 2005, *Harvey s.n.* (OSC).